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Phylogenetic placement of the enigmatic Floodplain water snake, *Lycodonomorphus obscuriventris* FitzSimons, 1964

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Lycodonomorphus is a genus of lamprophiid water snake endemic in Africa. Although widespread, abundant and presumably an important component of many aquatic and semi-aquatic food webs, these snakes are poorly understood taxonomically, particularly from a phylogenetic perspective. With only four of the nine species currently sequenced, this study attempts to improve our understanding of the evolutionary relationships within the genus through the phylogenetic placement of one of the most elusive species, *Lycodonomorphus obscuriventris*. Collected in the Ramsar declared Makuleke Wetlands in northern Kruger National Park (South Africa), the sample used in this study not only yielded the first DNA sequences for the taxon but also represented the most northerly South African record, bridging the gap between the southern and northern populations. The snake was sequenced for three partial mitochondrial genes (*16S, Cyt-b, ND4*) and one partial nuclear gene (*c-mos*) and phylogenetically placed, relative to the rest of the genus, using maximum likelihood (ML) and Bayesian inference (BI). Sequence divergences between sister taxa were also estimated using pairwise distance analysis. The concatenated phylogenetic reconstruction yielded similar topological structuring when compared to phylogenies from past articles, with both the ML and BI algorithms recovering strong support for *L. obscuriventris* as sister to a clade comprising of *L. whytii* + *L. laevissimus* + *L. rufulus*. The phylogenetic placement, albeit based on a single sample, challenges the original placement (morphological) of *L. obscuriventris* as sub-specific within *L. whytii*, suggesting that multiple species concepts should be considered when delineating species within this group.

Conservation implications: Prior to the discovery of the new record, the global distribution of *L. obscuriventris* was characterised by two disjunct populations. The new record bridges the distribution gap between these two populations, rendering the distribution continuous. This bodes well for the species as there is likely no barrier to gene flow, thereby buffering the species from localised threats given the more expansive distribution. Furthermore, given that the specimen was sampled from the Kruger National Park, the species is likely to be well-protected as much of its distribution within South Africa seems to fall within protected areas.

Keywords: Lamprophiidae; molecular systematics; water snake; range expansion; wetlands; African herpetology; Kruger National Park; Southern Africa.

Introduction

Lycodonomorphus is an endemic genus of medium-sized, semi-aquatic-to-aquatic lamprophiids occurring in south-central Africa that are characterised by their small heads, which are virtually indistinguishable from the neck (Branch 1998; Broadley 1983; Broadley & Blaylock 2013; Broadley, Doria and Wigge 2003; Marais 2004; Pietersen, Verburgt & Davies 2021; Spawls et al. 2018; Wallach, Williams & Boundy 2014). All species within the genus are oviparous, harmless to humans and do not possess enlarged fangs or venom glands (Branch 1998; Broadley 1983; Broadley et al. 2003; Marais 2004; Spawls et al. 2018). Whilst mostly nocturnal, several species in the genus forage actively during the day (Branch 1998; Broadley 1983; Kyle, Alexander & Du Preez 2021). Little is known about the ecology of these presumably important predators and their trophic role in aquatic habitats is largely underexplored (Madsen & Osterkamp 1982). Several studies (e.g. Kyle et al. 2021; Madsen & Osterkamp 1982; Raw 1973; Taylor 1970) have, however, reported members

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of the genus as feeding on fringes of water bodies for tadpoles, frogs, fish and other small vertebrates. Some of the more aquatic species have also been observed to ambush fish from amongst submerged rocks within waterbodies (Branch 1998).

Lycodonomorphus has undergone substantial taxonomic restructuring since the last major revision by Loveridge (1958), in which he only recognised four species with six subspecies. The genus currently contains nine accepted species (Uetz et al. 2022): *L. bicolor* (Günther, 1893), *L. inornatus* (Duméril, Bibron & Duméril, 1854), *L. laevissimus* (Günther, 1862), *L. leleupi* (Laurent, 1950), *L. mlanjensis* Loveridge, 1953, *L. obscuriventris* FitzSimons, 1964, *L. rufulus* (Lichtenstein, 1823), *L. subtaeniatus* Laurent, 1954 and *L. whytii* (Boulenger, 1897). Raw (1973) further described two subspecies, *L. laevissimus natalensis* and *L. laevissimus fitzsimonsi*, which were later synonymised with the nominate form (Haagner & Branch 1994).

Although currently recognised as a full species, the species has a complex origin (Broadley 1967, 1983, 1995; Rasmussen 2004). It was originally described as a subspecies of *L. whytii* based on the very dark ventrum, compared to the uniform immaculate white in the nominal form (FitzSimons 1964). Up until this point, however, *L. whytii* was considered a subspecies of *L. rufulus* (Loveridge 1958), necessitating the elevation of *L. whytii* to species level to accommodate the sub-specific recognition of *L. w. obscuriventris*. When Broadley (1967) reviewed newly collected material of *L. whytii* from central Mozambique, he found the ventral colouration to be variable and thus regarded them as the same species, although he did record differences in ventral and subcaudal scale counts. Based on this, scale differences and different habitat preferences, Broadley (1983) tentatively proceeded and recognised the southern material, including central Mozambique material, as *L. w. obscuriventris*. The discovery of a specimen that conforms to *L. w. obscuriventris* near the boundary of Lengwe Game Reserve in southern Malawi in 1995 raised interest in the taxonomical relationship between the two subspecies, especially because the type locality of the nominal form is from Fort Hill (= Chitipa) in northern Malawi (Broadley 1995). Based on morphological data gathered from the three *L. w. whytii* (1 Malawi, 2 Tanzania [all females]) type specimens available at the time, it was noted that *L. w. whytii* had lower ventral scale counts, higher subcaudal scale counts, it lacked the distinctive labial markings and displayed different habitat preferences (montane streams versus lowland floodplains) when compared to *L. w. obscuriventris* (see Broadley 1995). These results were expanded on with the incorporation of four additional specimens (including a male) of the nominal form by Rasmussen (2004). Based on these different traits, *L. obscuriventris* was then elevated to full species. Given the lack of phylogenetic work on the taxon, the species is considered related to *L. whytii*, given its past sub-specific placement and shared morphology (Broadley 1967, 1983, 1995; FitzSimons 1964; Rasmussen 2004). Although relatively widespread (Figure 1), with a distribution that stretches from eastern KwaZulu-Natal province (South Africa) into Eswatini, Kruger National Park, Zimbabwe and northern Mozambique into southern Malawi (Broadley 1983, 1995; Brown & Wilkey 2019; Kyle et al. 2021), *L. obscuriventris* remains elusive and poorly understood because of its original description.

Aim and objectives

Whilst the group has received much attention from traditional taxonomists (morphology), genetic work on *Lycodonomorphus* is severely lacking, with no dedicated phylogenetic study of the genus to date. The phylogenetic work that has included *Lycodonomorphus* spp. mainly focussed on the higher-level taxonomy (Pyron, Burbrink & Wiens 2013; Vidal et al. 2008; Zaher et al. 2019) and other closely related genera within Lamprophiidae such as *Lamprophis*, *Boaedon* and file snakes (Branch et al. 2019; Broadley et al. 2018; Ceríaco et al. 2021; Greenbaum et al. 2015; Hallermann et al. 2020; Keates et al. 2019; Kelly et al. 2008, 2011). Only limited representative sampling has been used for members of *Lycodonomorphus*, meaning only four of the nine species have been sequenced. These include *L. rufulus*, *L. inornatus*, *L. laevissimus* and *L. whytii*, with the last two species only having one sequence each (https://www.ncbi.nlm.nih.gov/genbank/). As stated in Vidal et al. (2008), the uncertainty over species boundaries within the *Lycodonomorphus whytii-mlanjensis-obscuriventris* complex needs to be addressed prior to the onset of systematic reordering in the group to ensure that taxonomical redundancies (e.g. synonyms, homonyms) are not incorporated into the nomenclature. To this end, we endeavour to improve our understanding of the phylogenetics of the group through the phylogenetic placement of *L. obscuriventris* using a recently acquired genetic sample of the species.

Research methods and design

Sample site and data collection

In early-April 2021, a multidisciplinary group of biologists embarked on a field survey of the Ramsar declared Makuleke Wetlands, in northern Kruger National Park, South Africa. The Kruger National Park itself forms a part of the Great Limpopo Transfrontier Park shared with Zimbabwe and Mozambique. The hydro-geomorphic setting of the seasonal pans was within the flood plain of the Limpopo and Luvuvhu River systems. The trip was focussed on surveying the food web dynamics of the temporary and permanent pans. On the 8th of April 2021, an inactive snake was discovered concealed beneath the bark of a large dead tree trunk lying on a small island in Banyini Pan. The snake was discovered approximately 2 km from the Zimbabwean border on the western limits of the Makuleke Contractual National Park (–22.365750, 31.075306) (Figure 1). The specimen was removed from the log and identified as *L. obscuriventris* based on colouration and more specifically the yellow upper labials

(Marais 2004). The specimen was humanely euthanised by placing it in a solution of clove oil until it was dead. Subsequently, a liver sample was dissected out for genetic analysis, and preserved in 99% ethanol. The specimen was then fixed in 10% formalin for 72 h after which it was transferred into 70% ethanol for long-term storage in the herpetological collection at the Port Elizabeth Museum (PEM), South Africa. The male specimen was catalogued under the number PEM R27786 and measured: 318 mm snout-vent length and 72 mm tail length (the terminal tip was slightly truncated).

Data analysis

DNA extraction, amplification and sequencing

DNA was isolated from the tissue sample with a standard salt extraction method (Bruford et al. 1992) using lysis (Buffer ATL) and elution (Buffer AE) buffers. Standard polymerase chain reaction (PCR) procedures were utilised to amplify one partial mitochondrial ribosomal gene (ribosomal ribonucleic acid [*16S*]), two partial mitochondrial genes (cytochrome b [*Cyt-b*] and NADH-dehydrogenase subunit 4 [*ND4*]) and one partial nuclear gene (oocyte maturation factor [*c-mos*]) (Table 1).

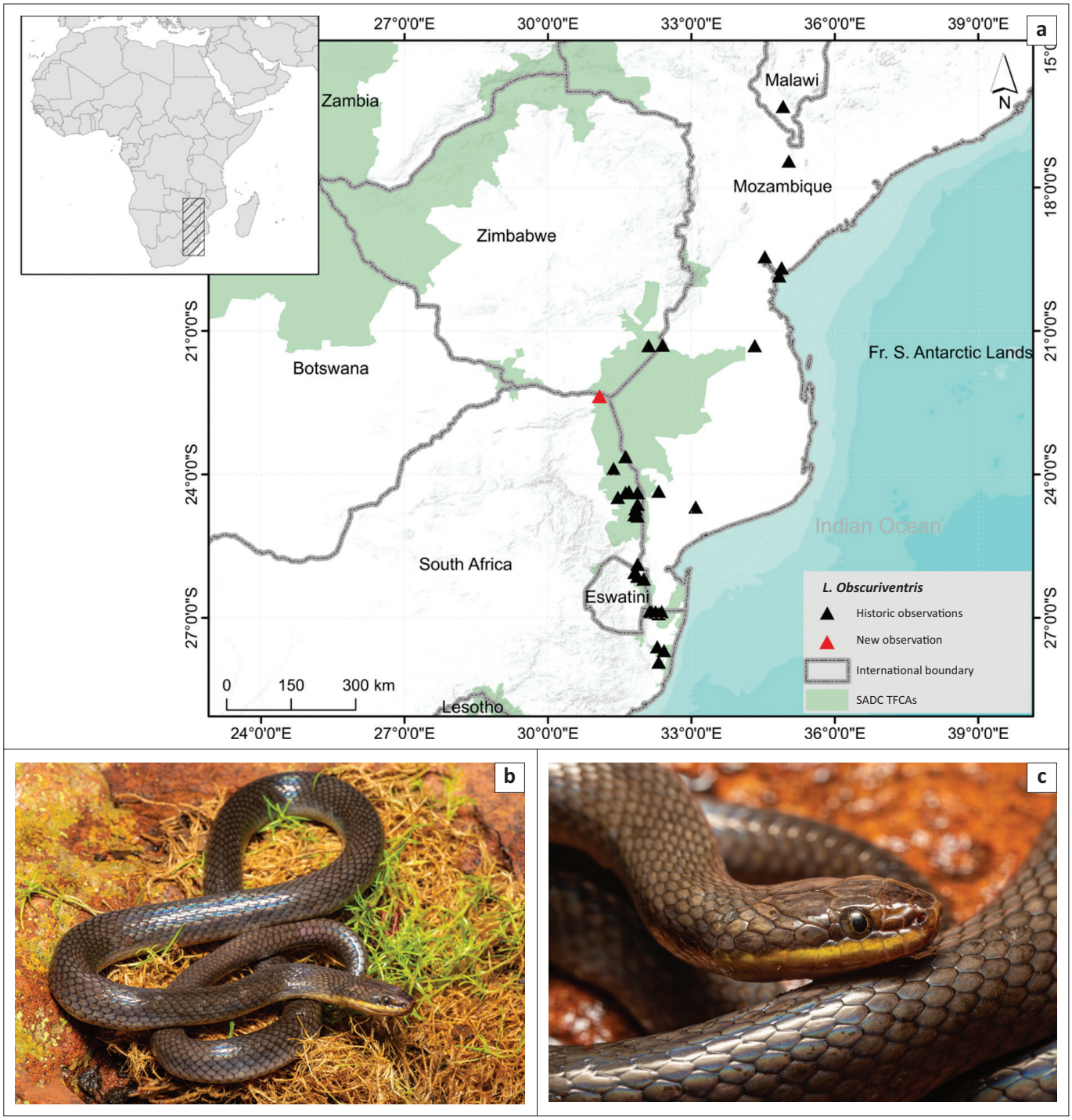

FIGURE 1: (a) Current global distribution of *Lycodonomorphus obscuriventris* with black triangles denoting historical localities and the red triangle denoting the new sample used in this study from the Makuleke Contractual National Park. (b) Full body photograph of PEM R27786. (c) Head shot of PEM R27786.

TABLE 1: Primers and PCR protocols used to generate sequences for the study.

Gene	Primer	Source	Annealing temperature (C°)
16S	L2510: 5′—CGCCTGTTTATCAAAAACAT—3′	Palumbi (1996)	50
	R1478: 5′—TGACTGCAGAGGGTGACGGGCGGTGTGT—3′		
Cyt-b	WWF: 5′—AAAYCAYCGTTGTWATTCAACTAC—3′	Whiting, Bauer and Sites (2003)	52
	Cyt-b-R2: 5′—GGGTGRAAKGGRATTTTATC—3′		
ND4	ND4: 5′—TGACTACCAAAAGCTCATGTAGAAGC—3′	Arevalo, Davis and Sites (1994)	56
	LeutRNA: 5′—CATTACTTTTACTTG GATTTGCACCA—3′		
c-mos	S77: 5′—CAT GGACTGGGATCAGTTATG—3′	Slowinski and Lawson (2002)	52
	S78: 5′—CCTTGGGTGTGATTTTCT CACCT—3′		

The PCR amplification was carried out using the primer pairs listed in Table 1. Amplification of the selected genes was carried out using 20 ng/µL – 50 ng/µL extracted genomic DNA. Each amplification was conducted with a PCR mixture to the total volume of 25 µL containing 12.5 µL Taq DNA Polymerase 2x Master Mix (Ampliqon; 3 mM $MgCl_2$, 0.4 mM dNTPs and Ampliqon Taq DNA polymerase), 2 µL forward primer (10 µM), 2 µL reverse primer (10 µM), 6.5 µL denucleated water and 2 µL genomic DNA. The cycling profile for all the genes was as follows: initial denaturing step at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 50 °C – 56 °C for 45 s and 72 °C for 45 s, with a final extension at 72 °C for 8 min. The prepared PCR products were sent to Macrogen Corp. (Amsterdam, Netherlands) for sequencing (after purification) with the forward primers only.

The phylogenetic placement of *L. obsuriventris* was estimated by comparing the genetic information of the newly collected sample with published sequences from all currently sequenced species of *Lycodonomorphus*: four *L. rufulus*, one *L. laevissimus*, one *L. whytii* and seven *L. inornatus* (Appendix 1). In addition to the ingroup taxa, the dataset was supplemented with sequences from closely related genera that were obtained from GenBank, to root the tree (Appendix 1).

Phylogenetic analysis

The sequence trace files were checked using BioEdit Sequence Alignment Editor v.7.2.5 (Hall 1999) and aligned with accessioned GenBank sequences using MEGA v.6.0 (Tamura et al. 2013) and the ClustalW alignment method. Prior to further analysis, the hyper-variable region of *16S* was removed. Four individual alignments were created and used to construct individual gene trees using the maximum likelihood (ML) algorithm (100 bootstrap replicates), and the GTR + G + I nucleotide substitution model. The individual consensus trees were used to determine the congruence of the topologies of the different genetic markers using the Congruence Index (I_{cong}; http://max2.ese.u-psud.fr/icong/index.help.html; Vienne, Giraud & Martin 2007). All gene-tree combinations were found to be congruent and a concatenated dataset of the four genes was created for additional phylogenetic analyses.

Saturation was tested in DAMBE v.6.4.67 (Xia 2013) using the individual as well as the combined first and second codon positions of each gene. Saturation was absent from every marker, necessitating the use of a gene-partitioned dataset for the phylogenetic reconstruction. The optimal partition scheme and best-fitting models of molecular evolution were selected using IQ-TREE v.2.1.2 (Minh et al. 2021) with the following settings: p-partition file (each partition has its own evolution rate), a greedy strategy and the FreeRate heterogeneity model excluded (only invariable site and Gamma rate heterogeneity considered) (Chernomor, Von Haeseler & Minh 2016; Kalyaanamoorthy et al. 2017). The greedy strategy implemented in ModelFinder via IQ-TREE v.2.1.2 resembles the one used in Partitionfinder 2 (Lanfear et al. 2016), in the way it starts the full partition model and subsequently merges two genes until the model fit no longer increases (Minh et al. 2021). The best-fitting model scheme selected included the following three partitions and models of evolution: TIM2 + I + G (*16S*); TIM2 + I +G (*Cyt-b, ND4*); GTR + I + G (*c-mos).* MrBayes v.3.2.7a (Ronquist et al. 2012) was not able to implement TIM2, so the next best alternative (GTR) was used in its place.

Phylogenetic tree and p-distance analysis

Maximum likelihood (ML) analysis was conducted using IQ-TREE v.2.1.2 (Nguyen et al. 2015). A random starting tree was used, and the ML analysis was assessed using the gene-partitioned scheme mentioned above and 1000 standard nonparametric bootstraps. Bayesian inference (BI) analysis (MrBayes v.3.2.7a; Ronquist et al. 2012) was implemented on the CIPRES Science Gateway XSEDE online resource (http://www.phylo.org; Miller et al. 2010; Tamura et al. 2013) using the best-fit nucleotide substitution models and partition scheme listed above. Two parallel runs of 20 million generations were performed, with trees being sampled every 1000 generations using BEAGLE (high performance likelihood calculation library). *Psammophylax rhombeatus* was used as an outgroup as only a single sample can be used as an outgroup using MrBayes. The number of generations discarded as burn-in was determined using Tracer v.1.6.0. (Rambaut & Drummond 2007). The effective sample size (ESS) was above 200 for all parameters and the runs reached convergence, indicating that a burn-in of 15% was adequate. Both trees were viewed in FigTree v.1.4.2 (Rambaut 2014).

Pairwise distance analysis was conducted in MEGA X (Kumar et al. 2018) using the *Cyt-b* alignment from the phylogenetic reconstruction. Sequences were grouped according to species and pairwise distance analysis was conducted on MEGA X, using uniform rates, pairwise deletion and 500 bootstrap replicates.

Ethical considerations

All procedures performed in this study followed all international, national and/or institutional guidelines for

the care and use of animals. Ethical permission was acquired from the University of Venda (reference number: SES/18/ERM/10/1009) and sample collection permits were acquired from the Kruger National Park (reference number: SKZ 132).

Results

Both phylognetic algorithms (ML and BL) showed strong support for the monophyly of *Lycodonomorphus* (bootstrap probability [BP] 91%, posterior probability [PP] 1.0) (Figure 2).

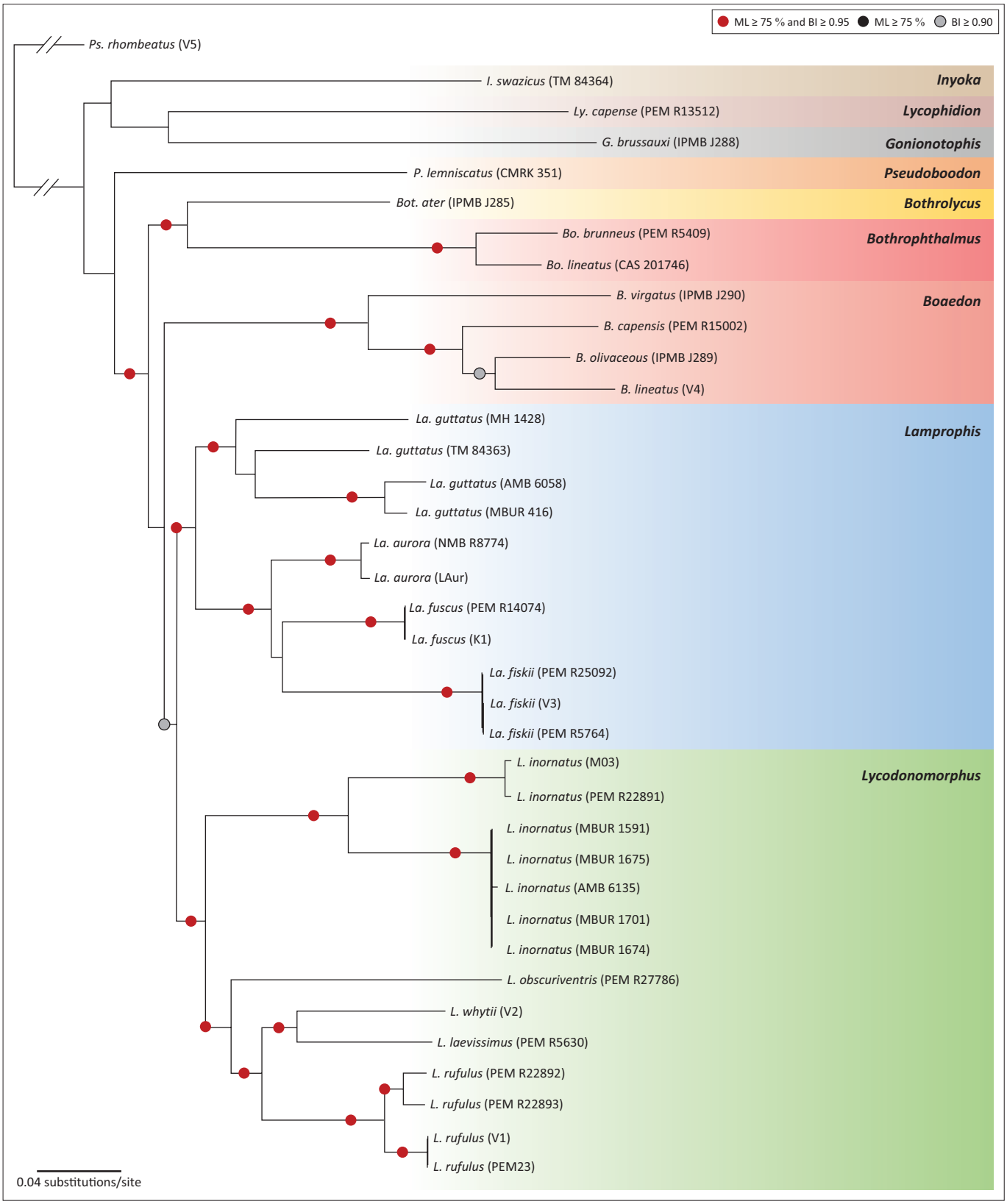

FIGURE 2: Maximum likelihood phylogenetic reconstruction with Bayesian inference support overlaid.

Lycodonomorphus obscuriventris was recovered as sister to *L. whytii* + *L. laevissimus* + *L. rufulus*, with strong support from both phylogenetic algorithms (BP 89%, PP 1.0). Furthermore, both algorithms recovered a supported sister relationship between *L. rufulus* and *L. whytii* + *L. laevissimus*. Both *L. rufulus* and *L. inornatus* were characterised by substantial topological sub-structuring with both algorithms recognising two supported clades in both species. Using *Cyt-b*, the average pairwise distance separating species within the genus was 15.88 ± 2.04% (mean ± standard deviation), whilst the average pairwise distance separating *L. obscuriventris* from other members of *Lycodonomorphus* was 15.87% ± 0.90% (Table 2). The lowest intrageneric pairwise distance separating *L. obscuriventris* was observed in *L. rufulus* (15.23%; Table 2). The structured clades observed within *L. inornatus* and *L. rufulus* (Figure 2) were supported by pairwise distance analysis with intraspecific divergences of 6.77% and 3.89%, respectively. Due to the lack of sampling for *L. laevissimus*, *L. whytii* and *L. obscuriventris*, intraspecific divergences could not be assessed for these species.

Discussion

Aside from the addition of *L. obscuriventris*, the phylogenetic reconstruction of *Lycodonomorphus* yielded identical topological structuring when compared to past publications (Kelly et al. 2011; Vidal et al. 2008; Zaher et al. 2019). Whilst only a single sample was available, the strong phylogenetic support (ML and BI) coupled with the divergent pairwise distance values separating *L. obscuriventris* from its congeners ratified the assertions of Broadley (1995) that the species is valid. Whilst the species was elevated out of the synonymy of *L. whytii* based on morphological and geographical grounds, the recovery of *L. obscuriventris* as sister to *L. laevissimus* + *L. rufulus* + *L. whytii* (Figure 2) suggests that the original sub-specific assignment of *L. obscuriventris* was erroneous and the current taxonomy reflects correct nomenclature.

The sister relationship between *L. laevissimus* and *L. whytii* is interesting to note given the large geographical distance separating the two species. *Lycodonomorphus laevissimus* is restricted to eastern South Africa, Lesotho and Eswatini, whilst *L. whytii* is found in northern Malawi and Tanzania (Branch 1998; Rasmussen 2004; Wallach et al. 2014). These findings would suggest that geographical proximity at least in southern Africa plays a reduced role in evolutionary relatedness. The topological structuring observed (Figure 2) may be better explained by the habitat preferences and associated ecologies of the different species with *L. obscuriventris* showing an affinity to lowland floodplains and pans, whilst *L. laevissimus* prefers slow moving streams, *L. whytii* prefers upland montane streams and *L. rufulus* being more generalist (Branch 1998; Rasmussen 2004).

Strengths and limitations

Whilst robust sampling was absent for many of the species in this study (only one sample each for *L. obscuriventris*, *L. whytii* and *L. laevissimus*), both *L. rufulus* and *L. inornatus* displayed intraspecific substructuring consistent with geographical variability. Within *L. inornatus*, the intraspecies diversity was 6.77% for *Cyt-b*. Whilst higher than the other species of *Lycodonomorphus*, it must be noted that seven samples (Kelly et al. 2011) were available for this study, five from Haenertsberg and two from the Eastern Cape. The large geographical distance separating the samples may explain the increased intraspecies diversity found with *L. inornatus*. The addition of new samples, representing the full distribution of the species, would thus likely support the recognition of *L. inornatus* as a single species, especially because the average interspecific divergence separating species is approximately 16%.

Implications or recommendations

In a recent study, Greenbaum et al. (2015) elevated the poorly known *Lycodonomorphus subtaeniatus upembae* (Laurent 1954) to full species status and transferred it to the genus *Boaedon*, whilst *Lycodonomorphus subtaeniatus* was retained, pending further phylogenetic evidence. The findings from this article coupled with the small morphological characteristics (mainly the lower number of midbody scale rows, simpler unforked-to-weakly forked hemipenis, no diastema separating maxillary teeth) separating *Lycodonomorphus* from *Boaedon* (Kelly et al. 2011) casts doubt on the validity of *Lycodonomorphus*, especially because several members of the genus show a strong terrestrial affinity (as opposed to being aquatic). For this reason, it is recommended that future work

TABLE 2: Sequence divergences (uncorrected pairwise distance values) separating the species of *Lycodonomorphus* and *Lamprophis* using cytochrome b (*Cyt-b*).

Species		1	2	3	4	5	6	7	8	9
1	*L. inornatus*	**6.77**	1.08	1.40	1.02	1.17	1.08	1.08	1.07	0.86
2	*L. laevissimus*	18.81	**NA**	1.44	0.95	1.11	1.05	1.17	1.18	0.93
3	*L. obscuriventris*	17.03	15.46	**NA**	1.29	1.64	1.40	1.41	1.45	1.27
4	*L. rufulus*	17.31	13.94	15.23	**3.89**	1.06	0.97	1.03	1.04	0.84
5	*L. whytii*	18.57	12.58	15.78	14.11	**NA**	1.19	1.24	1.20	1.09
6	*La. aurora*	16.94	14.77	15.38	14.61	16.24	**0.19**	0.98	0.95	0.83
7	*La. fiskii*	19.08	17.04	16.53	16.04	18.28	11.82	**0.07**	1.02	0.93
8	*La. fuscus*	16.88	16.26	16.86	14.51	15.54	10.56	13.70	**0.19**	0.90
9	*La. guttatus*	17.51	16.94	15.30	16.19	17.61	13.79	16.62	15.61	**11.67**

Note: Numbers in the diagonal (in bold) denote intraspecific divergences, numbers below the diagonal denote interspecific divergences and numbers above the diagonal denote the standard error of the interspecific divergences.

NA, not available.

on the group endeavours to sequence all the species associated with the genus to determine the most accurate systematic structuring of the group.

In addition to being the first sequenced sample of *L. obscuriventris*, the sample also represents the most westerly located record for the species and the most northerly located record for the Kruger National Park. The species' previous most northern record (within the Kruger National Park) was near the border of eastern Mozambique, approximately 30 km north of the Letaba River in the central Kruger National Park (Pienaar 1976). The newly collected specimen was found in the western reaches of the Makuleke Contractual Park approximately 150 km north of the previous most northern Kruger National Park record.

Conclusion

Prior to the discovery of the new records, the known distribution of *L. obscuriventris* was characterised by two disjunct populations, with a southerly population in eastern South Africa and Eswatini and a northern population in Zimbabwe, Mozambique and Malawi (Broadley, 1983, 1995). This sample, thus fills the gap between the two populations meaning that the distribution is likely continuous. Additionally, the recovery of the snake in the northern Kruger National Park bodes well for the conservation of the species as a large portion of its South African distribution seems to fall within this protected area, although this may be a result of sampling bias. Given the large proportion of records for this species inside the Kruger National Park, future effort should be directed to adjacent areas, including the Great Limpopo Transfrontier Park regions, to elucidate more clearly the ecology, biology and phylogeographic structuring of the enigmatic and elusive water snake.

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Competing interests

The authors would like to declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

C.K., R.J.W., T.D. and W.C. conceived the study. C.K. carried out lab work and genetic analyses. All authors contributed to the interpretation of the results. T.D., F.D. and E.S.R. arranged permitting and all other necessary permissions. T.D., F.D., R.W. and W.C. provided funding for the project. C.K. wrote the first draft of the manuscript. All authors provided a critical feedback and helped shape subsequent drafts of the manuscript.

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Data availability

The data that support the findings from this study are openly available on Genbank (https://www.ncbi.nlm.nih.gov/genbank/) and can be downloaded using the unique Genbank numbers found in Appendix 1.

Disclaimer

The views and opinions expressed in this article are those of the authors and do not necessarily reflect the official policy or position of any affiliated agency of the authors.

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Appendix 1 starts on the next page →

Appendix 1

TABLE 1-A1: List of samples used in the study.

Species	Sample Number	Source	Genes			
			16S	*Cyt-b*	*ND4*	*c-mos*
Lycodonomorphus rufulus	CMRK236/PEM R22892	Kelly et al. (2011)	-	HQ207111	HQ207153	HQ207076
L. rufulus	V1	Vidal et al. (2008)	FJ404199	FJ404299	FJ404374	FJ387200
L. rufulus	CMRK 478/ PEM R22893	Kelly et al. (2011)	-	HQ207118	HQ207160	HQ207081
L. rufulus	PEM23	Kelly et al. (2011)	-	HQ207144	-	HQ207102
L. laevissimus	PEM R05630	Kelly et al. (2009)	-	DQ486338	DQ486314	DQ486162
L. whytii	V2	Vidal et al. (2008)	FJ404200	FJ404300	FJ404375	FJ387201
L. obscuriventris	CK48/PEM R27786	-	OM413896	OM387031	OM387032	OM387033
L. inornatus	AMB 6135	Vidal et al. (2008)	AY611891	AY612073	FJ404367	AY611982
L. inornatus	MBUR 1701	Kelly et al. (2011)	-	HQ207134	HQ207176	HQ207093
L. inornatus	MBUR 1675	Kelly et al. (2011)	-	HQ207133	HQ207175	HQ207092
L. inornatus	MBUR 1674	Kelly et al. (2011)	-	HQ207132	HQ207172	HQ207091
L. inornatus	MBUR 1591	Kelly et al. (2011)	-	HQ207129	HQ207171	HQ207088
L. inornatus	M03	Kelly et al. (2011)	-	HQ207128	HQ207170	-
L. inornatus	CMRK 489/ PEM R22891	Kelly et al. (2011)	-	HQ207121	HQ207163	HQ207084
Lamprophis fuscus	PEM R14074	Nagy et al. (unpublished)	AY611894	AY612076	-	AY611985
La. fuscus	K1	Kelly et al. (2011)	-	HQ207127	HQ207169	-
La. aurora	NMB R08774	Kelly et al. (2011)	-	HQ207143	HQ207185	HQ207101
La. aurora	LAur	Kelly et al. (2011)	-	HQ207125	HQ207167	-
La. fiskii	V3	Vidal et al. (2008)	FJ404202	FJ404301	FJ404363	FJ387203
La. fiskii	DS03/ PEM R25092	Kelly et al. (2011)	-	HQ207124	HQ207166	HQ207087
La. fiskii	PEM R05764	Kelly et al. (2009)	-	DQ486354	DQ486329	DQ486178
La. guttatus	AMB 6058	Vidal et al. (2008)	AY611890	AY612072	FJ404366	AY611981
La. guttatus	TM 84363	Kelly et al. (2011)	-	DQ486355	DQ486330	DQ486179
La. guttatus	MBUR 416	Kelly et al. (2011)	-	HQ207135	HQ207177	HQ207094
La. guttatus	MH 1428	Kelly et al. (2011)	-	HQ207140	HQ207182	HQ207099
Boaedon olivaceous	IPMB J289	Vidal et al. (2008)	AY611862	AY612044	-	AY611953
B. capensis	PEM R15002	Vidal et al. (2008)	AY611895	AY612077	FJ404362	AY611986
B. lineatus	V4	Vidal et al. (2008)	FJ404205	FJ404303	-	FJ387205
B. virgatus	IPMB J290	Vidal et al. (2008)	AY611825	AY612008	FJ404369	AY611917
Bothrophthalmus brunneus	PEM R05409	Vidal et al. (2008)	AY611874	AY612056	FJ404348	AY611965
Bo. lineatus	CAS 201746	Vidal et al. (2008), Lawson (2005)	FJ404198	AF471090	FJ404349	FJ387199
Bothrolycus ater	IPMB J285	Vidal et al. (2008)	AY611859	AY612041	FJ404347	AY611950
Pseudoboodon lemniscatus	CMRK 351	Kelly et al. (2009)	-	DQ486350	DQ486325	DQ486174
Lycophidon capense	PEM R13512	Vidal et al. (2008)	AY611893	AY612075	FJ404376	AY611984
Inyoka swazicus	TM 84364	Kelly et al. (2009)	-	DQ486356	DQ486331	DQ486180
Gonionotophis brussauxi	IPMB J288	Vidal et al. (2008)	AY611861	AY612043	FJ404358	AY611952
Psammophylax rhombeatus	V5	Vidal et al. (2008)	FJ404215	FJ404312	FJ404327	FJ387215/